

SIBLING CANNIBALISM IN JUVENILES OF THE MARINE GASTROPOD *NASSARIUS FESTIVUS* (POWYS, 1835)

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INTRODUCTION

Shell-boring predation is well-studied in the prosobranch gastropods, including representatives of the Naticidae (Carriker, 1981; Kabat, 1990), Muricidae (Carriker, 1981), Buccinidae (Peterson & Black, 1995), Marginellidae (Ponder & Taylor, 1992; Taylor, 1998), and Cassidae (Hughes & Hughes, 1981). In contrast, representatives of the Nassariidae had not been found to bore into shells until Morton & Chan (1997) presented the first evidence of shell-boring predation by *Nassarius festivus* juveniles. Representatives of the Nassariidae are considered to be “the closest attempt of an obligate scavenging life style,” although members, including *Bullia digitalis* and *Ilyanassa obsoleta*, eat live prey (Britton & Morton, 1994). The findings of Morton & Chan (1997) were intriguing because the *N. festivus* adults are not shell borers, but scavengers, which descend readily and speedily on fresh carrion (Morton & Yuen, 2000), whereas the juveniles bore holes and cannibalize their siblings.

Offspring cannibalism of viable siblings in the study of trophic eggs has attracted much attention in such diverse taxa as sharks, non-social insects, frogs, spiders, and prosobranch gastropods (reviewed by Perry & Roitberg, 2006). For example, the sea whelk *Hemifusus tuba* feeds on trophic eggs, resulting in only a mean of 8.8 emerged as juveniles from a mean of 1,500 eggs laid in each capsule (Morton, 1987). Relatively little information is available on the gastropod juveniles that cannibalize similar-sized siblings. The aim of the present study is to provide empirical evidence of sibling cannibalism in *N. festivus* juveniles. The findings of Morton & Chan (1997) were obtained in a wholly accidental manner; some newly metamorphosed *N. festivus* left over an extended public holiday were dead and had their shells bored. The present study also answers the question of whether cannibalism was invoked by hunger.

MATERIALS AND METHODS

Collection and Maintenance of Experimental Animals

Approximately 100 adult *Nassarius festivus* (mean shell length $\pm$ SD: 7 ± 2 mm) were collected from a sandy shore at Lok Wo Sha, Tolo Harbour, Hong Kong (22°20'N, 114°10'E). Upon return to the laboratory, the adult gastropods were kept in a 13 l-fiberglass tank with well-aerated natural seawater of 33‰ salinity. Adults, egg capsules and larvae were maintained at 28°C, the measured temperature at the collection site. The clam *Tapes philippinarum* was opened and offered as food to the adult gastropods every other day. This food ration was shown to be able to maximize egg production (Cheung & Lam, 1999).

Egg capsules deposited on the aquarium wall were transferred to and maintained in a 1 l-glass beaker with 500 ml seawater. Membrane-filtered (pore size: 0.22 μ m) natural seawater (salinity 33‰) was used to maintain egg capsules and larvae and in the experimental procedures. Subsequently, hatched larvae were transferred to a 1 l-glass beaker and reared in seawater on a diet of the alga *Thalassiosira pseudonana* at 2×10^4 cells ml⁻¹ (Pechenik & Fisher, 1979). The antibiotics streptomycin and penicillin G were added at a concentration of 50 μ g ml⁻¹ each to control bacterial growth (Rittschof, 1984). The seawater was changed daily. Larvae that had completed metamorphosis and developed into crawling juveniles (characterized by a pair of tentacles and the resorption of vela) were removed from the glass beaker.

Experiment 1: Starvation

Sixty individuals that had metamorphosed on the same day were used in Experiment 1. Each newly metamorphosed individual was reared in a polystyrene Petri dish with 30 ml seawater

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renewed daily. There were two treatments. Three groups, each with ten individuals, were assigned to each of the two treatments as replicates. In the fed control groups, the juveniles were fed to satiation with *T. philippinarum* tissue daily; in the unfed groups, the juveniles were starved throughout the whole experimental period. The juveniles were examined every day, and those that did not respond to the stimulation of a pointed tip were considered dead. The experiment ended when all of the juveniles in the unfed treatment had died, at day 28 post-metamorphosis.

Experiment 2: Cannibalism

Similar to Experiment 1, 60 individuals that had metamorphosed on the same day were used in Experiment 2, also with two treatments and three replicate groups, each with ten individuals. Ten newly metamorphosed individuals in a group were, however, reared together in a polystyrene beaker with 300 ml seawater, renewed daily. Individuals in the fed control and unfed treatments received the same feeding or starving regimes as those in Experiment 1.

The shell length of each individual was measured every three days (e.g., on days 1, 4, 7 post-metamorphosis) under a stereoscopic microscope equipped with an eyepiece graticule at a magnification of 40X. As in Experiment 1, the juveniles were examined daily, and those that did not respond to the stimulation of a pointed tip were considered dead. Empty shells that appeared were collected and fixed with 4% (v/v) formaldehyde in autoclaved filtered seawater for further examination (i.e., whether they were intact, broken in half or in smaller pieces, or with a borehole). The experiment ended at day 28 post-metamorphosis.

Statistical Analysis

The normality of the data and homogeneity of variances were checked with Kolmogorov-Smirnov test and Barlett's test, respectively. Median lethal time (LT_{50}) was calculated for each replicate group using Probit analysis. Shell length data of all juveniles in a replicate group were first pooled together. T-tests were used to compare the mean LT_{50} and mean time for the first appearance of mortality of the unfed juveniles in Experiments 1 and 2 ($df = 4$ for all cases). The juvenile growth rates were compared using ANCOVA. The statistical tests were performed using the statistical software SPSS 11.0.

RESULTS

Experiment 1: Starvation

In the experiment in which the juveniles were kept separately, all fed control individuals survived 28 days post-metamorphosis (Fig. 1). In contrast, mortality of the unfed juveniles first occurred on day 8, with the mean time for the first appearance of mortality among the replicates being 12 ± 3.5 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles). No unfed juvenile survived beyond day 28. Furthermore, the mean LT_{50} for the unfed group was 16.8 ± 3.5 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles).

Experiment 2: Cannibalism

When the juveniles in a replicate were kept together in the same aquarium, all fed control juveniles survived 28 days post-metamorphosis (Fig. 2). In contrast, mortality first occurred on day 3 for the unfed juveniles, with the mean time for the first appearance of mortality among replicates being 3.7 ± 1.2 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles). This mean time was significantly shorter than the mean of the unfed group from Experiment 1 ($t_4 = 3.95$, $P = 0.017$). Of the unfed individuals, only 17% survived to the end of the experiment (Fig. 2). Furthermore, the mean LT_{50} for the unfed group was 15.2 ± 3.4 days post-metamorphosis (1 SD) ($n = 3$, each with a group of ten juveniles). This mean was not significantly different from the mean of the unfed group from Experiment 1 ($t_4 = 0.58$, $P = 0.595$).

The control juveniles increased their mean shell length of 0.93 ± 0.03 mm (1 SD) at day 1 to the mean of 2.41 ± 0.33 mm (1 SD) at day 28 post-metamorphosis (in both cases, $n = 3$, each with a group of ten juveniles) (Fig. 3). The unfed juveniles increased their mean shell length of 0.90 ± 0.02 mm (1 SD) at day 1 ($n = 3$, each with a group of ten juveniles) to the mean of 1.33 ± 0.20 mm (1 SD) at days 25 and 28 post-metamorphosis (in both cases, $n = 3$, each with a group of one to three juveniles). The change in the mean shell length of the unfed juveniles between each data point was positive up to day 25 post-metamorphosis (Fig. 3).

Both fed and unfed individuals grew at the same slow rate for the first ten days, to about 1 mm (ANCOVA: $t_{20} = 0.09$, $P > 0.5$). Thereafter they diverged. The fed individuals grew significantly faster than the unfed individuals between days 10 and 28 (ANCOVA: $t_{20} = 9.32$, P

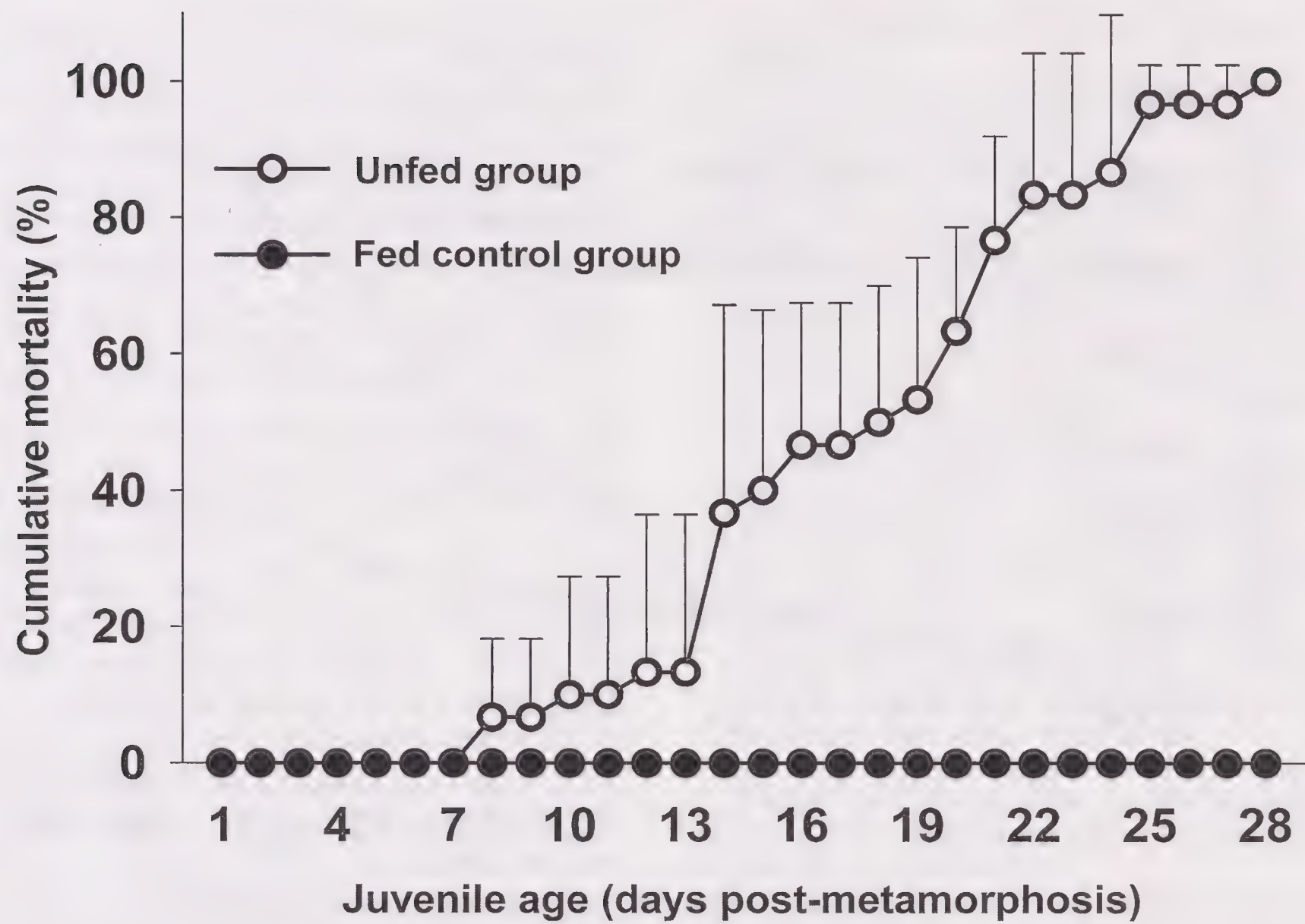


FIG. 1. Experiment 1. Cumulative mortality of fed and unfed *Nassarius festivus* juveniles. Each data point represents the mean (+ SD) of three replicates, each with a group of ten juveniles; juveniles in a replicate were kept separately.

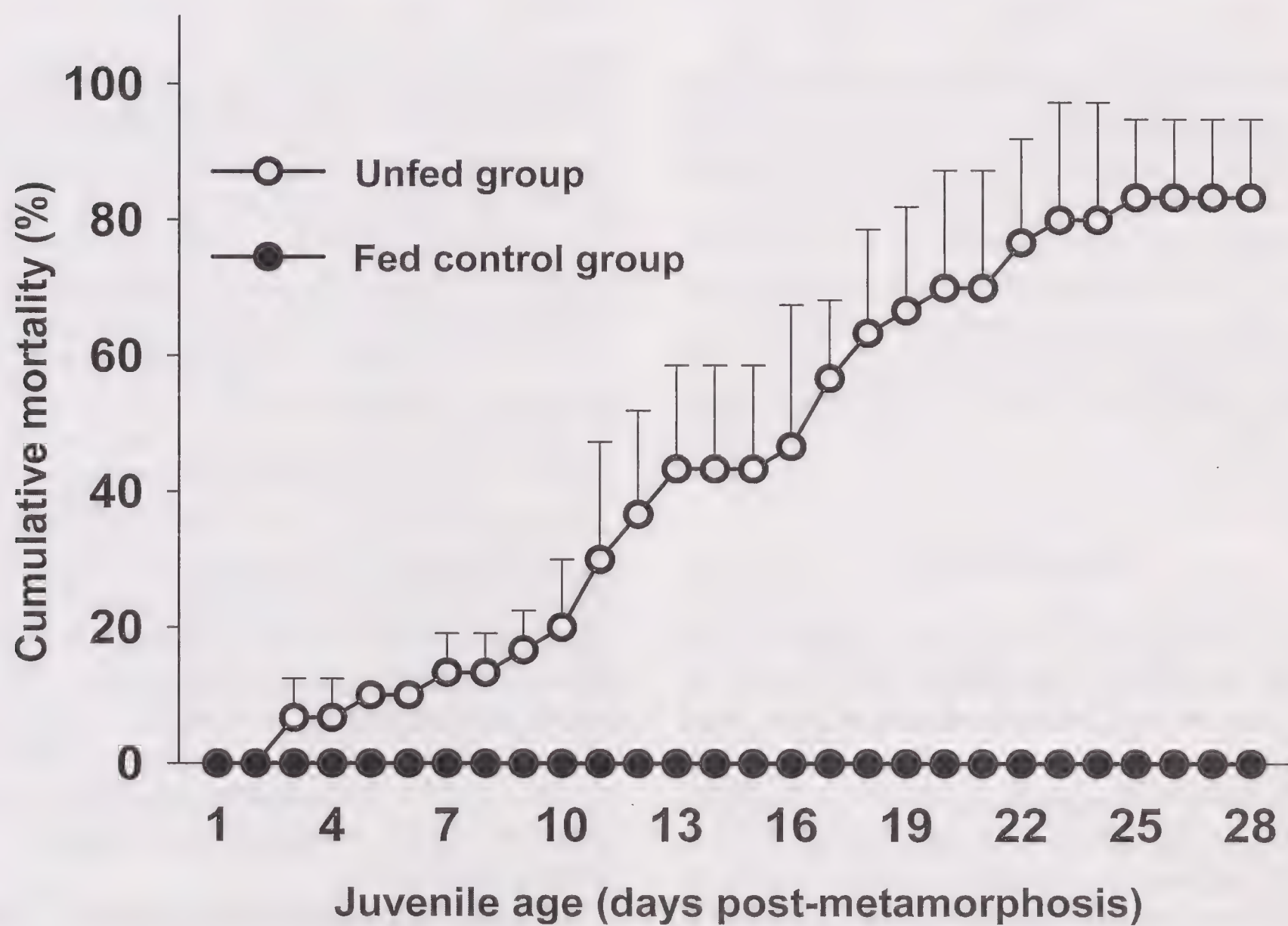


FIG. 2. Experiment 2. Cumulative mortality of fed and unfed *Nassarius festivus* juveniles. Each data point represents the mean (+ SD) of three replicates, each with a group of ten juveniles; juveniles in a replicate were kept together in the same aquarium.

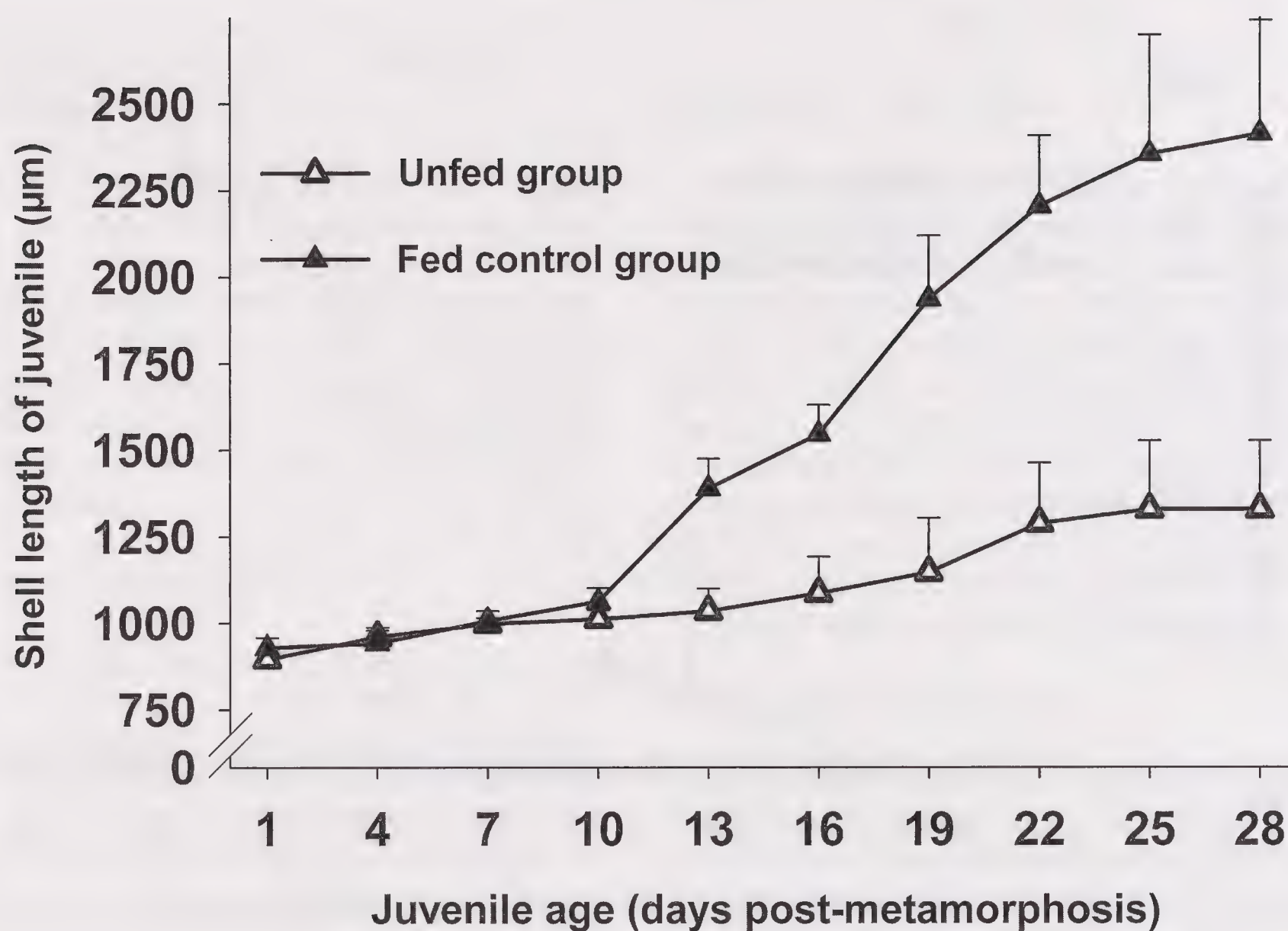


FIG. 3. Experiment 2. Mean shell length of *Nassarius festivus* juveniles. Each data point represents the mean (+ SD) of three replicates, each with a group of one to ten juveniles; juveniles in a replicate were kept together in the same aquarium. The shell lengths of all juveniles in a replicate were first pooled together.

< 0.001). The growth rates of both fed and unfed groups also increased after the first 10 days (fed group – ANCOVA: $t_{29} = 2.05$, $P < 0.05$; unfed group – ANCOVA: $t_{29} = 4.39$, $P < 0.001$).

Among the 25 empty shells of the unfed *N. festivus* juveniles examined, 18 of them had intact shells with no observable damage or scars, three had broken shells in halves or in smaller pieces and four had a borehole on their shells.

DISCUSSION

This present study provides experimental evidence of sibling cannibalism in *Nassarius festivus* juveniles. Firstly, mortality of the unfed juveniles first occurred on day 3 post-metamorphosis when these juveniles were kept together in the same aquarium (the mean time for the first appearance of mortality = 3.7 days; Fig. 2). In contrast, mortality first occurred on day 8 when unfed juveniles were kept separately (the mean time for the first appearance of mortality = 12 days; Fig. 1). These results suggest that mortality due to non-starvation cause, most likely, takes place long before the occurrence

of mortality due to starvation. Secondly, positive growth in the mean shell length of the unfed juveniles up to day 25 post-metamorphosis in Experiment 2 indicates energy gain from cannibalized siblings or sibling carrion (Fig. 3). Thirdly, 17% of the unfed individuals survived to the end of Experiment 2, in which juveniles were kept together, while none survived after the same experimental period in Experiment 1, in which juveniles were kept separately. Survivorship of the unfed individuals was enhanced because of sibling cannibalism. Finally, broken shells, as well as boreholes, were found among the empty shells of these individuals. The unfed juveniles attacked other individuals and broke their shells into two or more pieces in Experiment 2 (personal observation). Results of the present study, along with those of Morton & Chan (1997), demonstrate that at least one member of the Nassaridae engages in shell-boring predation.

The present study also suggests that cannibalism was not a generalized strategy, but invoked only during periods of starvation in the newly metamorphosed *N. festivus*. The well-fed juveniles that were kept together in the same aquarium all survived 28 days post-metamor-

phosis, indicating no mortality due to cannibalism (or any other causes) (Fig. 2). Polis (1981) attributed cannibalism to the unavailability of alternate prey. As predicted by foraging theory, an animal may expand its diet beyond the normal limits of acceptable prey during periods of hunger or limited food (Polis, 1981). This study found that the *N. festivus* juveniles bored holes and cannibalized their siblings when they lacked carrion to scavenge. Fed juveniles did not bore, because clam carrion was readily available and was, thereby, less energy-consuming to obtain. The juveniles might also be injured when they attacked their siblings.

Cannibalism may enhance the survival of an individual during the transition time needed to discover natural prey (Morton, 1987). The present study demonstrates that cannibalism allowed 17% of *N. festivus* juveniles to survive to day 28 post-metamorphosis (in contrast to 0%). The importance of cannibalism as an alternative feeding strategy among these well-known scavengers to their species success or fitness may reflect the fact that carrion is only ephemerally and infrequently available to scavengers (Britton & Morton, 1994). Feeding is further restricted in *N. festivus* as individuals retreat into the sand when tides ebb. Morton (1987) and Dietl (2003) suggested that small population size and dispersal of siblings would, however, make cannibalism an ineffective juvenile survival mechanism because cannibalism may decrease the species success or fitness by removing potential reproductive partners. It is not known if population size and sibling dispersal have been important to the evolution of cannibalism in the Nassariidae. Nonetheless, cannibalism could be an effective mean of persistence during times of low food availability.

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